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The Behavior of the Bottle-nosed Dolphin (*Tursiops truncatus*): Mating, pregnancy, parturition and mother-infant behavior[1]

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(Plates I-III; Text-figure 1)

Introduction

Because Cetacea bear their young in water, data on the normal progress of pregnancy and parturition, together with information on mating behavior and post-natal development, have been either lacking or only incompletely available to biologists interested in these animals. The greatest part of the information as yet recorded has been received from whalers and other sea-faring men who have observed these animals in the open sea, where conditions are far from ideal for such observations (Lütken, 1888; Pedersen, 1931; Slijper, 1936). James (1914) first observed the birth of a Common Porpoise (*Phocaena phocaena* (Linnaeus) in captivity in the Brighton Aquarium, but this was a stillbirth. Khvatov (1938) and Sleptzov (1940) both observed what they believed to be normal births in the Common Dolphin (*Delphinus delphis* Linnaeus) in shallow portions of the Black Sea, or in large seines in which a number of animals were confined prior to being drawn toward shore. McBride & Hebb (1948) and McBride & Kritzler (1951) were the first, however, to record their observations under conditions almost ideal for this purpose.

In their 1951 paper, McBride & Kritzler published on this subject the latest data taken at Marine Studios, Marineland, Florida, where the activities of the Bottle-nosed Dolphin (*Tursiops truncatus* Montagu) in a 75-foot circular tank may be viewed conveniently through portholes set in the walls. At that time five pregnancies resulting in normal births had been under observation. Three animals had conceived in the tank. Since then five additional pregnancies, all resulting in normal births, have been observed, providing many additional data. The present report is based upon a series of observations instituted by one of us which was conducted over a period of slightly more than three years, and which for the last year and a half was on a daily basis. During parts of the latter portions of these observations, both authors were able to be at Marineland at the same time, and observations could be made almost constantly, so that a steady daily record was kept which provided the observers with continuous data, not only on the group as a whole but also on the activities of any individual animal.

Up to the time of the 1951 paper by McBride & Kritzler, new animals were introduced at irregular intervals and some deletions were made in order to keep the population at a desirable level and at the same time to minimize the possibilities of combat which resulted on a previous occasion in injuries to a newborn dolphin (McBride & Kritzler, 1951). Since then, the colony has become a stabilized and self-perpetuating group, in which the only additions are those by birth. This fact has enabled the observers to obtain data on the growth and maturation of several individuals. One of the females born in the tank has reached the beginning of her eighth

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year and terminated her first pregnancy in March, 1954.[3]

Table 1 shows the names, sexes, dates of birth and relationships of the members of the stable population of the tank. In addition, Happy, a fully-grown adult male, and presumably the father of all the infants conceived in the tank, was present throughout the three years covered by the present data. Frank and Floyd, born in the tank, were removed in December, 1953.

actively sought the company of the selected female by such stratagems as chasing her when she left him, hovering over her when she hunted for fish or was otherwise occupied in one spot, and by returning to her immediately after both had been engaged in other activities, such as feeding. Such exclusive companionship lasted from three or four days to several weeks.

This period of prolonged companionship often, but not always, led to further activities on

Table 1. Stable Population of *Tursiops truncatus* in Tank at Marine Studios.

Date of Birth	Sex of Infant	Name of Infant	Name of Mother	Duration of Birth*	Remarks
Feb. 26, 1947	Female	Spray†	Mona	28	
April 23, 1948	Male		Mrs. Jones	21	Died of injuries
May 8, 1949	Male	Algie†	Susie	117	
May 12, 1950	Male	Frank	Pudgy		
May 15, 1950	Male	Floyd	Mrs. Jones		
Feb. 7, 1953	Female	Mamie	Mona		Died June 13, 1953
Feb. 23, 1953	Female	Maggie	Mrs. Jones		
Feb. 27, 1953	Female	Nellie	Susie		
May 7, 1953	Male	Mitch	Pudgy	68	Died Feb. 22, 1954
March 4, 1954	Female	Peggy	Spray	48	Died March 19, 1954

*Duration of birth of infant in minutes, from first appearance to complete emergence. Where no figure appears, the birth took place at night and was unobserved.

†These animals were conceived in the wild before the capture of the mother. All other infants in the table were conceived in the tank.

Precopulatory Behavior

In the spring of 1952, 1953 and 1954 (February to May inclusive), there occurred a number of special activities which appeared to be the preliminaries to copulation, since the copulatory pattern was frequently seen to follow them. The aggregate of these activities over a period of time between two animals of opposite sex we term courtship. It should be understood that not all of these activities need necessarily take place between any two particular animals, and further, that they need not follow any particular order.

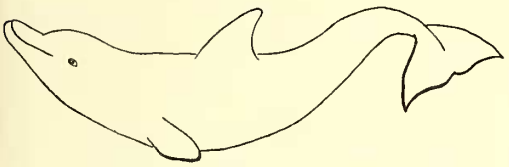
During the major portion of the year the adult male changed his companions often, swimming with one animal for a few minutes or a few hours, and rarely remaining with it for more than a few days. His companions during this time were other males, females or young animals of either sex. He also remained alone for long periods. During the early spring, however, he showed preference for the company of one particular female and remained with her for prolonged periods. He either accepted the presence of other animals or avoided them, but he

the part of the male, depending on the attendant circumstances. At times, without any further activity, the male suddenly broke off the partnership and shifted his attention to other interests, and there was no further association between the male and female for weeks or months. On the other hand, he often suddenly increased his attention to her and engaged in activities which were more aggressive and more directly associated with precopulatory behavior. These activities were quite varied and included posturing, stroking, rubbing, nuzzling, mouthing, jaw clapping and yelping. Any or all of these were included in any sequence and varied in intensity, becoming most intense just before exhibition of the copulatory pattern.

Posturing. — Although this type of act appeared at any time during precopulatory behavior, it was usually one of the first indications, aside from prolonged companionship, that precopulatory activities were about to become more intense. The male swam toward the female and took up a position in front of her, or slightly to one side, but well within her line of vision. He then bent his body in such a way that from the side it took on the shape of an S-curve, head pointing up, flukes down, as in Text-fig. 1. He maintained this position for about two to five seconds, and then resumed normal swimming.

[3]This paper was submitted for publication on February 13, 1956.

The action was repeated immediately, after several minutes, or not at all, depending on the female's general responsiveness and the other activities taking place in the tank. All males postured sometimes, but males were seen to begin courtship without posturing. Therefore it appears to be a subordinate portion of the precopulatory pattern of behavior. Although posturing was usually shown by the male, it was observed in the female under certain circumstances which will be described later.



TEXT-FIG. 1. Male dolphin in posturing position.

Stroking. — During normal swimming the male took up a position just behind and below the female. When this happened, the female often altered the normal motion of her flukes in such a way as to stroke or lightly pat the head of the male as she swam. At times the positions were reversed, and the male stroked the female's head. The stroking motion was easily distinguished from the normal swimming motion, and also from the lashing of the flukes given by another animal in an attempt to avoid contact or to get away. Such action on the part of the two animals was usually assumed when they were resting, and was the least vigorous and energetic of the sexual activities. At other times either male or female swam in such a way as to bring one or both flippers in contact with some part of the other's body (Pl. I, Fig. 1), and by swimming along or across the other's body produced a stroking effect. Another form of the same activity took place when one of the animals turned on its back and, swimming beneath the other in the same direction and at the same speed, moved its flippers rhythmically back and forth across the other's body. The other member of the couple responded by repeating the action at the some time so that the two sets of flippers stroked each other. Such actions could, of course, be continued only until it was necessary for one or the other to rise to breathe, but it was resumed immediately following this, and with interruptions for respiration was sometimes continued for half an hour or more. Stroking was also carried out by gentle movements of the head against the body of the partner. Another variation took place when one animal placed itself beside or beneath the other, and stroked the genital area of the partner with the tip of one fluke.

Rubbing. — This was a much more strenuous action in which one member, usually the male, swimming at a fast pace, advanced upon the female and rubbed part of his body vigorously against hers (Pl. I, Fig. 2). This advance took place from any direction relative to the two animals, but was most dramatic when the male approached the female head on, as if to engage in a head-on collision, and then turned aside at the right moment and just enough to produce vigorous contact of the two bodies along their lengths. This type of inter-animal contact rarely lasted for more than a few minutes, during which the male made repeated rushes at the female. Trumpeting and whistling sounds were sometimes heard during this time. The female sometimes turned after each rush and swam toward the male as he repeated the maneuver, enhancing the vigor of each contact, or she rushed away, leaping out of the water in a real or apparent attempt to escape. When the latter took place, the male usually rushed to the spot where she was to reenter the water and rubbed energetically against her as she did so. (Pl. I, Fig. 3).

Nuzzling. — Nuzzling took place when one animal applied its closed snout to some part of the body of the partner and moved it around in that area. Although this action took place in a number of other situations, such as the nuzzling which goes on between mother and infant, the male often nuzzled at the genital area of the female, possibly as an investigative measure, and also possibly stimulating her thereby. The female, at times, nuzzled the male in the same way.

Mouthing. — (Pl. I, Fig. 4) Mouthing was an activity similar to nuzzling, but took place with the mouth open. Although used during precopulatory activity in the same manner as nuzzling, it also took place in other ways. When in an appropriate position, one animal took a flipper, fluke or sometimes even the head or snout of the partner between the teeth (Pl. I, Fig. 4), and gently closed the mouth upon it, thereby holding the part. This grasp was a gentle one, and was released as the partner pulled away, without leaving tooth marks or gashes. This is in contrast to the grips taken on each other by two fighting males, which result in deep cuts and gashes inflicted by the sharp teeth. Either nuzzling or mouthing of the male's genital region by the female sometimes resulted in an erection.

Jaw Clapping. — At times during the companionship of the male and female, a second

male interfered in the relationship between them, either by swimming between the two, separating them, or by nuzzling the female while she swam with the first male. In such a case, the male's response was rapid and often violent. He is able, by clapping his jaws together forcefully, to produce a sharp loud sound, which can be heard at a distance of fifteen feet or more from the outer wall of the tank. As early as 1940, McBride recognized this sound as "the principal form of intimidation" when produced by a dominant animal. Often jaw clapping was sufficient to discourage the intruder, but if not, the first male resorted to violent lashes with his flukes, sometimes throwing the offender against the side of the tank with tremendous force; or he actively attacked the intruder with his teeth, inflicting serious gashes upon the other's flukes, flippers, back and head. Jaw clapping was also used if the female swam away for a short time, or if another female interfered. In these cases, however, the final results were rarely violent, since the partner rejoined the male immediately, and an interfering female hastily left. In other situations, jaw clapping was used by non-dominant animals as a sign of displeasure and not necessarily as intimidation.

Yelping. — During the more intense stages of precopulatory behavior, another sound, characteristic of this situation, was often heard in the tank. This sound has been interpreted to be a type of mating call (Essapian, 1953; Wood, 1953). It was a high-pitched yelp, delivered as a series of short sharp cries. The number of yelps in a series varied from two or three to seven or eight, and the series might be repeated after an interval of about fifteen seconds, or might not be repeated for a much longer interval, depending upon the circumstances. There can be no doubt that the male produced these sounds, since when he was in the proper position relative to the observer, the flap of the blowhole and the area behind the blowhole could be seen to move as if they were being depressed at the time that the sound was heard. No bubbles escaped from the blowhole with the production of this sound. The male yelped very rarely when he and the female were swimming quietly together. On the other hand, if the female strayed away from his vicinity, or stopped to investigate another animal or an object in the tank, in the majority of cases the male promptly produced a series of the yelping cries and continued to do so at short intervals until the female returned to him. If she did not respond at once, he continued to yelp until she did. Immediately upon her return to him the yelping ceased. If another female responded, she was ignored. Since, as far as the investigators could determine, yelping was heard only during the mating season, and the selected female responded, it is felt that the interpretation of this sound as a mating call is valid.

Although the male consistently swam with a single female during the earliest days of the spring season, the most intense of the precopulatory activities did not take place at this time. Such activities seemed to begin shortly after the birth of the first infant of the year, and evidence is accumulating that true precopulatory activity may be triggered by this birth. In 1953, the first infant was born on February 7, and the first display of intense sexual activity on the part of the male, accompanied by yelping, was seen three days later. Since no observations were taken on the two previous days, it may have taken place even earlier. In 1954 the first infant was born on March 4, and the beginning of yelping and intense sexual aggressiveness on the part of the male began the same afternoon. Since the March date is quite late in the year for the appearance of the first infant, and continuous observations were carried out through all of February, it can be seen that there was a possible connection between the two events. However, more evidence is necessary to establish a clear relationship between them.

The pattern of the male's sexual activities previous to copulation was not a consistent one. Any or all of the actions described above were involved, and any or all of them could take place within an hour or two. On one day the male engaged in each of them and periods of intense activity alternated with periods when the two animals swam quietly together for an hour or more. On another day he persistently engaged in one of them, rubbing for instance, though the entire day, and displayed none of the others, resting only a few minutes at a time before resuming his activity.

Initiation of precopulatory behavior by the female.—The part of the female in a paired situation was less energetic than that of the male. When she was the chosen companion, it was only rarely that she engaged in any but the mildest of precopulatory activities toward him. She swam close to him, perhaps maintaining contact with him by an extended flipper touching his body, and she was occasionally seen to initiate mild stroking activity. She actively cooperated with him, however, when he initiated the more intense actions, and there was one occasion when she actively took the lead. As mentioned above, during the height of the rubbing activity on the part of the male, she often

rushed away from him at great speed, and leaped far out of the water, perhaps to escape his attentions. On such occasions, he sometimes joined her in her leaps, but more often he swam rapidly to the spot where she was expected to enter the water, where he rubbed against her even more energetically as she came down. This sequence of events was often repeated a number of times before both animals reverted to swimming together quietly. Since after such activity the female immediately rejoined the male and continued to swim close to him, and because copulatory activity often followed such a display, it is possible that the display aroused more intense activity on the part of the male.

In the case of an unpaired female, however, the situation was quite different. At various times an unpaired female was seen engaging in somewhat unusual activities, such as scraping her ventral side along the bottom of the tank on the coquina gravel, and rubbing her genital area vigorously and repeatedly over the brushes, which are set up in the tank as back-scratchers for the animals. These actions have led the observers to suspect that such a female was in a state of high sexual receptivity, and in some cases this opinion has been confirmed by her subsequent actions. An unpaired female in this state often postured before the male, and sometimes initiated stroking and rubbing activities. She approached him from all angles and attempted to maintain physical contact with him. She was often very persistent in these activities even though the male paid no attention to her. She nuzzled and mouthed his genital region, and this latter behavior was sometimes followed by an erection on his part. If this happened, she often stationed herself within his line of vision and remained motionless in the water, her ventral side toward him as if inviting his attention. If he did not respond, she sometimes repeated some or all of these actions. In addition, she sometimes sought out the younger of the two males, who just reaching maturity, and initiated these activities with him. Since this younger male was often rejected as a sexual partner by the mature females, he usually responded to such attentions, and if he did so, the female allowed him to begin copulatory behavior. Such a female was seen to hang motionless and almost vertical at the surface of the water with only her blowhole exposed, while the younger male persistently engaged in copulatory behavior. Uusually he was not completely successful. At times, the mature and dominant male was attracted to the scene of this activiy, and paricipated in it himself, in which case the two males alternately approached the female.

Copulatory Behavior

The males exhibited erections during the more vigorous phases of sexual activity. Erection and the copulatory pattern often followed the leaping display of the female or a period of strong rubbing.

The copulatory activities which have been observed may be divided as follows: erection, approach, intromission, ejaculation, and withdrawal.

Erection.—The penis of the Bottle-nosed Dolphin erects suddenly (1 to 2 seconds), the body of the organ curving outward and ventrally from the genital slit in which it is ordinarily enclosed, followed by the tip which springs rapidly away from the body. The erect penis is directed craniad, and deviates from the longitudinal axis of the animal an estimated 20 degrees to the left.

Approach.—Because of the sinistral deviation of the penis, the male usually approached the female on her right side, and partially rolling on his right side, brought the penis close to her genital opening. He approached from the rear and parallel to her, at an angle perpendicular to her path, or at any angle between these two extremes. He swam toward her, dorsal side up, rolling over as he approached her, or he turned on his back at a distance and swam toward her in that fashion. Sometimes he approached from her left side but this was unusual.

At his approach, the female did any of three things. Sometimes she swam away from the male, or continued swimming at his side, without changing her position or speed. In both of these cases, entry was almost impossible, and the male usually desisted after a short time. At other times, she rolled over on her left side and presented her ventral side to the male, at the same time slowing her speed. This position allowed the male to effect penetration more easily.

Intromission.—(Pl.I, Fig. 5) When the male was close to the female, with his ventral surface approximating hers, he brought the erect penis into contact with her ventral side in the region of the vagina. This contact was often repeated many times before intromission was achieved, since both animals were swimming slowly throughout, and other animals and water currents sometimes caused the copulating pair to move apart. If there was no outside interference, and the female matched her speed to that of the male, intromission was effected. In most of the cases seen by the present observers, the penis was inserted no more than to half its length into the vagina.

Pelvic thrusts were often observed, both before and after intromission was effected. They usually began as soon as the ventral side of the erected penis came into contact with the ventral side of the female. They continued only as long as the contact was maintained, and at times did not occur until penetration took place. A series of these thrusts usually lasted for two or three seconds, but the series was sometimes repeated a number of times. The intromission lasted for not more than ten seconds, after which withdrawal took place.

Ejaculation.—The observers do not know whether ejaculation took place during intromission, since the animals could not be captured and sperm counts made. On one occasion, after a partial intromission of short duration such as those mentioned above, the animals broke apart suddenly, and a stream of milky fluid was ejected into the water from the penis of the male. It is thought that this was semen.

Withdrawal.—After an intromission lasting from two to ten seconds, the animals broke apart suddenly. Each righted itself and swam normally. The penis at this time was still erect. Often the male made a new approach immediately, and the above activities were repeated. Sometimes the penis withdrew suddenly into the genital slit and the two animals swam off in different directions. At other times the copulatory pattern was repeated at intervals of one to seven or eight minutes for a half hour or more.

The greatest part of copulatory activity by the bull took place at night or in the early hours of the morning. It is not certain whether the reason for this lay in the diversions created during the day by feeding periods or whether it was the result of nocturnal preferences by the animals. In the past when there were fewer feeding periods the animals also tended to copulate at night. Their behavior in the wild in this respect is, of course, unknown.

Just after dawn on March 1, 1953, a member of the Marine Studios staff reported seeing a copulation between an adult male and a mature female. Although he did not observe the two coming together, he reported that the male swam on his back beneath the female. The ventral surfaces were closely pressed together so that the penis of the male was not visible. This position was retained for about thirty seconds. When the pair broke apart, the penis of the male was erect. No traces of the ejaculate were seen in the water. Since the female involved produced an infant the following spring, it is possible that it was at this time that conception took place. This, of course, is far from certain and such data can be used only to narrow the time of conception to within a week or two, since the female was paired with the male during that period of time.

The single instance described above was of longer duration and there was complete penetration of the penis. Those seen by the present observers were of shorter duration and involved partial penetration. The observers were not able to determine whether the single instance was a typical copulation and the others incomplete, or whether a short copulation with partial penetration is typical and the single instance atypical.

There were certain complicating factors involved in such observations, since other animals were attracted to the site of copulatory activities. Young males, particularly, exhibited erections and competed for the female by crowding and pushing one another aside. In addition to interfering with the copulating animals. they also effectively obscured the view of the observers.

Behavior During Gestation

Since the report of McBride & Kritzler (1951) five conceptions have taken place and the resulting pregnancies have been carried to completion, each terminating in the birth of a normal healthy infant. Four of these were recognized during the latter months of the gestation period. These resulted in the four births during the spring of 1953. The fifth (1954 birth) was recognized as a possibility from the time of conception, and its progress recorded throughout.

"Spray," a young female, was born at Marine Studios on February 26, 1947, and was the first normal infant porpoise born in captivity. She was, from the first, a healthy animal and despite bruises and lacerations inflicted on the day of her birth by sexually aroused males in the tank, she grew and progressed normally. She was a gregarious animal, and learned early to participate in all of the activities of the other animals, as well as to respond to the attentions of human beings when members of the staff played with her. Although McBride & Kritzler believed that she might initiate her first pregnancy in the spring of her fourth year, it was not until the spring of 1953 (the beginning of her seventh year) that this event took place.

On February 10, 1953, the only adult male dolphin in the tank began to show a persistent interest in Spray, and continued to seek her company for the following 13 days without eliciting any interest on her part. He was heard yelping on several occasions, also without any response

from her. He continued his pursuit of her, and on February 23 they were seen swimming together for prolonged periods for the first time. At this time the "courtship" took on what might be considered a typical pattern, including all the types of precopulatory behavior described in the previous section. Yelping by the male was often heard and Spray responded to it during this period. In addition, Spray was often seen leaping out of the water, followed by the male who persisted in keeping in close physical contaet with her. No erections were seen during this activity. Early on the morning of March 1, it was reported that the bull and Spray were seen copulating. No further such incidents were reported, although it is probable that others took place. The two kept up their close association until about March 9, when it was observed that they were no longer constantly together. During the several days following this, the association was abandoned except for occasional short contacts, and for the remaindcr of the spring season the two animals were rarely secn together, each seeking the company of other dolphins. The male was seen either alone or in the company of other females. Spray reverted to her most consistent occupation, swimming with one or another of the new infants.

In the spring of 1949, a male infant was born to another of the adult females. From the time of his birth, Spray was almost constantly in his company, and took on the role of playfellow, not only to him, but to all of the later infants born in the tank. She often remained with them when their mothers were at the feeding platform, and was often seen swimming about the tank with them when their mothers were otherwise occupied. It was natural, therefore, that she should continue this occupation with the infants born in 1953, and she continued in these activities well into the summer.

It has been reported in McBride & Kritzler (1951) that during the latter half of pregnancy, the female tends to withdraw from association with others. In the case reported in that paper, two females, both pregnant, spent most of their time together, apart from the rest of the tank population. In the present case there were no other pregnant females present. Although Spray was often sought out as a companion by other members of the tank community, she showed an obvious preference from her earliest days for the company of her mother, "Mona," and this preference has continued to the present. Therefore, when she began to withdraw from the company of the other animals, she sought her mother as a companion. The first sign of this association, which was to continue throughout her pregnancy, was seen on June 27. On that day it lasted for only a short time, but was repeated on July 1, July 3 and again on July 7. Thereafter it became a more regular companionship, and the time Spray spent with Mona gradually increased from a few minutes a day till, toward the end of her pregnancy, almost all the time she spent in company was with her mother. The remainder of the time in company was spent with "Pudgy," another mature female, and her recent infant, "Mitch" with both of whom Spray had spent much time since the infant's birth in May, 1953. Although closely observed throughout, it was seldom after July 8 that she was seen in the company of any other animal, and when such instances occurred, they lasted for brief periods only. It was also noted that in most of these instances, the other animal involved approached Spray, while she displayed little interest in seeking out other company. At this time and thereafter throughout her gestation, it was also noted that her activities decreased in vigor, and she adopted habits that were slower and more leisurely.

On June 30, the increasing roundness of her abdomen was noted for the first time, and although the animals have been known to gain and lose weight for various unknown reasons, at this time the possibility of her pregnancy became, in the minds of the observers, a probability. Pl. II, Figs. 6 & 7, show the difference in contour between a non-pregnant dolphin and one in a late stage of pregnancy.

On October 2, it was noted for the first time that Spray's mammary glands showed perceptible growth, and the area just forward and on each side of the genital opening, which had heretofore been rather flat and undemarcated from the surrounding region, now became rounder and fuller, as the glands increased in size. This definition of the glands became greater as term approached, although the glands never reached the size of those of some of the other mature, laetating females.

On December 9, straining or body flexion was observed for the first time in this pregnancy. Straining always occurred when the animal was in the horizontal position, often when she was swimming. If the animal was resting at the surface she remained there, with only the blowhole out of water. If she was swimming below the surface, she usually came to a complete halt. The flukes and caudal peduncle moved ventrally (Pl. II, Fig. 8), and as the flexion reached its maximum, the tail approached an angle of 45 degrees from the horizontal, forming an angle with the body of about 135 degrees. Often the head also bent ventrally, and as the strain

reached its climax, the entire body formed an arch, and the muscles appeared to be taut. This position was held for a few seconds. When the animal relaxed, the tail passed the horizontal and was raised dorsally, where it was held up at an angle almost as great as in the other direction (Pl. II, Fig. 9). This recurved position was also held for a few seconds, and then the animal relaxed again and swam off in normal fashion. The arch might occur without the recurve but the recurve never took place alone. Although body flexion has been seen in animals other than pregnant females, it is most noticeable in such females, and is considered a characteristic action in the latter months of pregnancy because of its repeated appearance. It was not until January 12 that Spray was seen straining again, but after this date it was seen often. From the beginning of February, flexions were seen to occur at the rate of about one a day, gradually increasing in frequency until the rate was two or three a day by the middle of the month. Toward the end of February, the total number of flexions per day increased, and the pattern changed substantially. During this period Spray might go through an entire day during which no flexions were seen by the observers, while on another day she could be observed to strain almost continuously for an hour or more, about two or three minutes elapsing between flexions. A period without flexions then followed, succeeded in turn by another period in which straining was frequent. This pattern continued until just before the birth took place, and as term approached, the periods of flexion succeeded each other with decreasing periods between until just before term, when Spray was recorded as straining almost continuously throughout several hours every day. On the morning of the day before she gave birth, she was seen to flex seventeen times in thirty-seven minutes.

As term approached, there were also other activities in which Spray was seen to participate, and which were not usually seen in non-pregnant animals. In a number of instances, she came down over the brushes which were anchored to the floor of the tank and applied her ventral side to them, scratching vigorously. At times she was seen to actually insert some of the bristles into the genital opening and wriggle back and forth over them. She also glided down to the piles of rocks on the floor, and as she approached them, she lowered the posterior end of her body, so that she bumped her ventral side against them with considerable force. Twice she did this with such force that large rocks were displaced. The activities could, perhaps, be correlated with increased vaginal irritation or tension.

During the latter months, Spray's size increased considerably, especially in the abdominal area. Although porpoises, which are exceedingly streamlined animals, do not show the distortions in body shape exhibited by some other animals during late pregnancy, even casual visitors to the exhibit were able to observe her greater girth and often commented upon it. At this time her navel, which is normally a slightly depressed scar, became slightly elevated from the body surface. Formerly a fast and graceful swimmer, she became at times almost clumsy in her body movements.

Several weeks before the birth Spray was observed to change her habits of respiration. She frequently rose to the surface, and hovering there, respired a number of times in succession, the total time elapsed being about two or three minutes. Thereafter, she resumed normal swimming. A minute or two later the behavior was repeated. This might be followed by an interval of normal breathing. As term approached the unusual breathing pattern became more frequent, and consequently she came to spend most of her time swimming at the upper level of the tank quite close to the surface. Only occasionally did she descend to the floor, usually to rub herself over the brushes or rocks. During this time she was also observed to open her mouth widely at intervals, as if yawning, and she sometimes projected her tongue beyond the tip of her upper jaw, as if licking it. She did this while beneath the surface of the water, and its significance is unknown.

At this time there was also an increase in the number of defecations per day. This number increased until during the last few days before birth defecation was almost continuous. Normally the animals defecate after feeding, and occasionally between feedings. Since the feces dissipate rapidly into the water, it was difficult to estimate the amount, but it is believed that the total amount of feces was also increased. It is probable that the increased numbers of both respirations and defecations were caused by pressure of the growing uterus upon the other internal organs. Feeding continued normally throughout this time and through the day preceding the birth.

During the last few weeks, any exertion on Spray's part produced another visible sign that parturition was not far off. During flexions, or during the spurts of vigorous swimming in which she occasionally indulged, the vaginal opening, ordinarily a closed slit, was seen to dilate to a width of about a half inch to an inch (Pl. II, Fig. 10). As term drew near, these dilations became more frequent and also more pronounced. The

opening widened to approximately two inches and the dilation sometimes lasted as long as five to ten seconds before relaxation set in.

During this last month the movements of the infant inside Spray's abdomen were easily seen. At times, distinct bulges could be seen on various parts of her abdomen, bulges which shifted from place to place, sometimes in a matter of seconds. When this happened distinct movements could be observed which were not due to the action of the mother's muscles. When a particularly violent movement of the foetus took place, she often halted abruptly and waited in mid-stroke until the movement had stopped and the foetus was quiet again. On February 4, a bulge appeared on her abdomen, posteriorly and ventrolaterally on the right side. This was persistent, lasting for several days. On February 13, Spray's contours changed again, and evidently the foetus was now situated more anteriorly than had previously been the case, since bulges were seen on both sides in the anterior part of the abdomen. Later the foetus shifted more to the left, and on February 23 an area on her left side just behind her flipper was noticeably protruding. This condition persisted until the time of parturition.

Parturition

On the morning of March 4, both observers were called to the tank at 5 a.m. The birth was observed to begin at 4:55 a.m. by a member of the Marine Studios night crew, who had been previously alerted as to the imminence of the event. Spray was seen swimming slowly and normally around the tank with her mother, Mona. The flukes of the infant were protruding from the vaginal opening and were lying in a horizontal plane. Most of the other animals in the tank were acting normally, and only when one of them came close enough to touch Spray or the baby did she speed up or swim evasively. At 5:15 a.m. the flukes turned at right angles to their former position, and the infant was seen to be lying on its left side. At 5:20 a.m. about three-quarters of the caudal peduncle had emerged. As she swam, Spray flexed mildly and the foetus emerged still further, but as she relaxed, it receded again. The situation continued in this way until 5:40 a.m., when the entire length (about 14 inches) of the caudal peduncle had appeared. Pl. II, Figs. 11 & 12, show two stages of birth. At this time Spray was still swimming slowly, but in a normal fashion, with Mona. At 5:43 a.m. there was suddenly a great deal of excitement in the tank. The animals gathered in the center amid whistling and a variety of other noises. Although banks of lights had been set up in the event of a birth at night, the excited racing of the animals and the flurry of bubbles in the water which this produced, plus the darkness of the hour, kept the observers from seeing what took place during the exact instant when the infant fell free from the mother. The infant was first seen at the surface a few seconds later, against the light at the far side of the tank. The total time elapsed was 48 minutes. A minute or two later the animals had again broken up into groups, and the infant, a female, was seen swimming uncertainly, but energetically, between the dorsal fins of Spray and Mona. The baby's dorsal was inclined to the left and her flippers and flukes were soft and flabby. A number of vertical creases without pigment were seen along her sides. This is characteristic of newborn dolphins. A few minutes later, at 5:47 a.m., the adult male, possibly aroused by the birth, gave chase to Mona, and her place beside the baby was taken by Pudgy, the other female which had spent much time with Spray during her pregnancy. Shortly thereafter, however, the bull turned his attention to Pudgy, and Mona returned to swim with Spray and the infant. These three continued together, and the two adult animals guarded and guided the new infant throughout the first days of its life.

As soon as it became light, the skin of Spray's abdomen was seen to be patterned in a series of fine wrinkles, as in crêpe paper. Probably this was the result of the strong contraction of the muscles beneath, which resumed their normal tonus before the skin could do so. The crêpe paper effect lasted for several days before it disappeared.

At 9:15 am. Spray, who had been swimming slowly with the infant and Mona, suddenly speeded up and raced across the tank. This was the first rapid swimming she had done for several days, and as she did so the placenta emerged from the vaginal opening as though forcibly expelled. There was no blood visible as it was ejected, and Spray paid no further attention to it. Immediately after the placenta was expelled, Spray slowed down again, and swam off with the baby. She did not approach the placenta again.

At 10:55 a.m. the new infant began to nuzzle her mother's side. Spray neither slowed down nor rolled over at this time. At 11:18 the baby nuzzled again, this time more persistently, but without success. Again Spray did not cooperate. At 1:00 p.m., however, Spray rolled over on her side and adjusted her speed so that her mammary region was close to the baby's snout. The infant displayed no reaction to this, and did not nurse. At 1:22 p.m. the baby nuzzled again. This time Spray rolled over, and after several

thrusts of her snout, the infant found the nipples, and suckled successfully for the first time (Pl. III, Fig. 13). Another nuzzle a minute or so later was unsuccessful, but others shortly thereafter and later in the afternoon showed that the young one was locating her objective more rapidly. Within 24 hours she was seen to suckle regularly without any preliminary searching.

In 1953, the year previous to the parturition just described, four other births occurred. Each of these produced a normal, living infant. All the conceptions took place in the tank at Marine Studios. There were certain features in which each differed from the one just described.

During the last few days of January, 1952, Mona was observed to be spending most of her time with the adult bull porpoise, and was reported in copulation with him at that time. Shortly thereafter, she ate very little for a period of almost a month, although still in the company of the bull. She remained with the bull through most of February, although observations indicate that during the latter half of February it was Mona who sought the bull's company, rather than the reverse.

It was only in November, 1952, that her increased size attracted attention to her condition. On February 6, 1953, Mona's abdomen showed a shallow, concave area ventrally between the region of the navel and that of the mammary glands, which could be seen only when viewed from the side. Anterior to this region the distension of her abdomen was conspicuous. This concavity did not appear on Spray, and its significance is not known, though it may be concerned with the position of the foetus in the uterus. Some time during the night of February 6, a female infant was born to Mona, and when first seen the next morning, she was swimming between the dorsal fins of Mona and Spray. By that time the dorsal fin of the infant was already stiffened and upright, so that it could not be determined to which side it had inclined. Also, the placenta had been passed, and the baby was suckling regularly. The infant showed five deep transverse creases on the left side, six on the right. All of these were much lighter than the rest of the animal. The skin of Mona's abdomen showed the fine wrinkles which are characteristic of the new mother.

Although "Mrs. Jones," a mature female, was not observed to spend more than a day or two with the bull in the spring of 1952, abdominal distension in November of that year made it evident that she, too, was pregnant. On February 14, 1953, she was reported to be straining and dilating her vaginal opening. During this month she spent most of her time either alone or with Pudgy. On three occasions before the birth, Mrs. Jones showed flexion and on two of these dilations were also observed. She showed no concavity in the posterior abdominal area. On February 23, she gave birth to a female infant during the afternoon. When the infant was first seen, shortly after 4 p.m., its dorsal was inclined to the right. The mother showed the characteristic wrinkling of the abdominal skin.

On February 11 and 18, 1952, the bull's courtship activities were observed to be directed toward "Susie," another female, and she responded to his yelps. In November it was noted that Susie was pregnant. On February 6, 1953, the shallow concavity was seen on her abdomen. This persisted until she gave birth. During the latter months of her pregnancy, Susie was not accompanied by another female, but swam alone and avoided the company or contact of any other animal. She flexed intermittently during the month before parturition and her genital slit dilated when she strained or when she broke into a rapid swim. She was also seen to defecate often and copiously during the last few days before birth.

Early on the morning of February 27, she gave birth to a female infant, whose dorsal fin was inclined to the right. Susie was not accompanied by any other female on the morning of the birth in spite of attempts made by Pudgy to remain near her, and she cared for the infant without the aid of any other animal. This was quite unusual, considering the conduct of all the other mothers on which data are available.

Late in April, 1952, Pudgy was seen in the company of the bull for several days. It was not until April, 1953, that her pregnant condition was suspected. Although she was the stoutest animal in the group, her weight was well distributed over her entire body, and the roundness of her abdominal region was not outstanding. Her previous pregnancy had gone unsuspected until May, 1950, when she gave birth to a male infant. Therefore, when her size increased in April, 1953, and especially when she avoided the company of other animals, she was again suspected of being pregnant, despite the absence of other symptoms.

On May 5 and 6, Pudgy was seen in the company of Spray, but with no other animal. On the 6th, she flexed a number of times. On the morning of the 7th, she strained almost continuously, and between flexions rose to the surface where she hung, respiring frequently in a pattern similar to that shown by Spray. At this time the shallow concave area was seen on her abdomen. During the afternoon of the 7th, Pudgy gave

birth to a male infant. The birth began at 2:30 p.m. when two or three inches of the baby's flukes were seen to emerge immediately after a strong flexion. At this time Mrs. Jones was swimming beside Pudgy. The following outline, extracted from the notes taken on the day of the birth, give a clear picture of the events during this parturition.

2:30 p.m. Pudgy arches and recurves. Suddenly there appear approximately 2-3 inches of the baby's flukes. Pudgy contracts abdominal muscles.

2:35 p.m. Pudgy swimming slowly in center of tank. 3-4 inches of flukes showing. Flexion.

2:37 p.m. Flukes completely visible. Horizontal, but tips curled ventrally.

2:38 p.m. Pudgy swimming close to floor of tank with Jones. She flexes and recurves. Other animals nosing around at distance of 2-3 feet.

2:40 p.m. Pudgy almost scrapes the bottom with her ventral side. Slows down till barely moving.

2:43 p.m. 2 inches of caudal peduncle showing. Pudgy maintains steady unhurried rate of speed.

2:45 p.m. 3 inches of caudal peduncle emerged. Jones with Pudgy.

2:47 p.m. Pudgy flexes. Spray swims just behind and below Pudgy, her head pointing upward.

2:50 p.m. 4-5 inches of caudal peduncle have emerged. All other animals quiet. Pudgy strains.

2:51 p.m. Foetus slips back an inch or two.

2:55 p.m. Foetus has turned, now lies on its right side.

2:57 p.m. Pudgy swimming close to surface and wall.

3:02 p.m. 5-6 inches of caudal peduncle have emerged.

3:07 p.m. Feeding show in progress. All animals rushing around.

3:08 p.m. Diver feeding underwater. All animals feeding except Pudgy, who swims in circles away from points of disturbance. Pudgy alone. Infant's tail hangs limp.

3:15 p.m. Still 5-6 inches of caudal peduncle showing.

3:22 p.m. 7-8 inches of caudal peduncle showing. Pudgy swims slowly, flexes.

3:27 p.m. Foetus slides partially out and then recedes as Pudgy flexes and relaxes. Pudgy is alone, swimming short circles in N. E. corner of the tank.

3:36 p.m. Pudgy now with Jones. Still 7-8 inches of caudal peduncle are all that can be seen of infant.

3:38 p.m. Pudgy flexes again, and recurves strongly, swimming partially on her right side. At this point, less than an inch of the baby's dorsal becomes visible, and in the next 4-5 seconds, the foetus is expelled, followed by a stream of blood.

Contrary to previous reports (McBride & Kritzler, 1951) Pudgy did not whirl as the infant was expelled, but continued swimming on and up toward the surface. The umbilical cord broke as it pulled taut. As in the case of Spray, all the dolphins gathered at the point where the birth took place, whistling and producing a clamor of other noises. Mrs. Jones pushed the baby out of the way of the other animals. Then she placed her snout beneath it and gave it one thrust toward the surface, where it took its first breath, 5 or 6 seconds after its birth. It is well known that infant dolphins are able to reach the surface without assistance immediately after birth (McBride & Kritzler, 1951), and there is no reason to suppose that this infant was an exception, especially as it was seen swimming immediately after the nudge. As a normal infant, it would undoubtedly have reached the surface for its first breath unaided, and the push given by Mrs. Jones was of secondary importance. Spray positioned herself on the other side of Mrs. Jones and the infant swam between their dorsal fins, Pudgy trailing behind. This situation continued for the next two or three minutes, when Pudgy moved into position beside the baby, and Mrs. Jones dropped out. The infant was energetic as it labored to keep pace with the adults. The baby's dorsal was inclined to the left. The total time elapsed in this birth was 68 minutes.

Behavior of Mother and Infant

As stated by McBride & Kritzler (1951), and confirmed in later cases by the present observers, the newborn dolphin remains very close to its mother during the first month. During the first few days while its swimming is still uncertain, particularly in regard to direction, the infant will often stray slightly, but the mother invariably swims toward it and pushes it gently, guiding its direction until it is close to her side again, usually next to her dorsal fin. This position close to her dorsal fin is maintained by the infant during its first month or two, and gradually the baby then becomes accustomed to what the observers consider the typical rest position, under the mother's tail, with the top of its head lightly touching her abdomen. During the first few weeks, at least, the infant sleeps in the position next to the mother's dorsal fin.

The mother does not allow the young infant to come into close contact with other animals, and when one approaches, will swiftly sweep the young one away with her, usually placing it on the side away from the intruder.

After about two weeks the infant begins to swim about its mother and vary its position in relation to her. It may dart around her head, slip under her tail, or swim beside her at a distance of a foot or two. However, if the young one increases the distance between them to as much as ten feet, the mother will immediately swim toward it and reorient it toward her. At feeding time, the new mother will guide her infant to a position a few feet from the feeding platform, where she leaves it swimming in a small circle. She will approach the feeding platform and secure one fish, then rush back to the baby. Often she will not approach the platform again, but spend her time with the infant on the side of the tank opposite to the feeding platform, maneuvering herself and her infant away from dolphins who race for food thrown on the surface of the water. Because of this situation, special feedings are often provided for new mothers, who will accept fish thrown to them while swimming with the offspring after the regular feedings are over.

The four young ones born in 1953 prospered and grew quickly. Nursing began promptly and all the calves were able to find the nipples rapidly within 24 hours after birth. They suckled in the general pattern noted by McBride & Kritzler (1951), three to nine times within as many minutes, followed by an interval of 10 to about 25 or 30 minutes.

At about two weeks of age all the babies began to move away from their mothers, and were repeatedly retrieved. As mentioned under Spray's behavior during pregnancy, she spent a good deal of her time in the company of the young dolphins. From the time they were less than a month old, she was seen swimming with them and their mothers, and often swept away each of them with her in a rapid trip around the tank. If any other animal came close to one of the infants, the mother promptly showed her displeasure by slapping the intruder with her flukes, or by swiftly removing the calf from his vicinity. However, each mother soon allowed Spray to escort her infant without evidence of concern, and Spray usually returned the infant to its mother within a minute or two.

When Spray had been accepted as a trusted escort for the infants, all the mothers occasionally left their calves in her company while they were occupied at the feeding platform, and she was often seen surrounded by two, three or four youngsters at this time. In addition, one mother could sometimes be seen guarding a group of infants while the others fed (Pl. III, Fig. 14). The mother who had received her food then returned and relieved the escort so that she could get her share. At the end of feeding time, each mother retrieved her own calf, and there was never the slightest hesitation about picking her own infant from the group. No mother was ever seen to make a mistake and choose the wrong infant.

By the time they were six weeks old, the young dolphins were swimming away from their mothers regularly, and associating with each other or some of the adult animals. Their mothers, by this time, had relaxed their vigilance somewhat, and the infants were no longer kept within a few feet at all times, although they were still kept under close watch. A short excursion or play period was usually followed by a longer rest period spent under or close to the mother. The infants began to show an interest in the objects and fishes in the tank and were seen to investigate, and if small enough toss about, any new object which came to their attention. If the object was a familiar one in the tank, a bit of rock, a turtle, or a small fish, the mothers watched nearby while the calf investigated, and sometimes joined it. However, if the object was an unfamiliar one, such as a new animal, or an object dropped by a visitor, the mother displayed agitation and set up a loud and continuous whistling while steering the young one away, and only when she had removed the baby from the disturbing object did she resume her normal behavior. This extreme vigilance and care were typical of the dolphin mother during the first months of her infant's life, and continued in somewhat lesser degree throughout at least the first year.

In direct contrast to the above situation, Spray showed a distinct lack of care toward her infant born in 1954. At first the situation seemed normal. The baby began to nuzzle her mother's side, as stated above, five hours after birth, and it was 2 hours and 27 minutes after this initial effort that she began to suckle. After this, nursing proceeded successfully, and the baby suckled in the same general pattern as the above infants. The baby seemed to be in good health and swam strongly from the first.

After a few days, however, it was seen that she was not growing as other infants had done. Newborn dolphins lose their thin appearance quickly, and after a few days their necks become less distinct and their abdomens become rounded. This was not true in the case of Spray's infant.

In addition, Spray did not care for the baby

as vigilantly as other mothers had done. She remained at the feeding platform throughout almost the entire feeding, returning to the calf only once or twice during this five- or six-minute period. The infant was alone during this time, except for the momentary visits of her mother.

On March 13, Spray's infant attempted for the first time to swim away from her mother. Spray and Mona swam after her, but did not hurry to her side. This, too, was in contrast to the conduct of other dolphin mothers. On March 14, the baby persistently left Spray and swam among the other animals. If she strayed more than about twenty feet away, Spray brought her back, but if she stayed within this distance, no attempt was made to restrict her movements. Twice, however, when she strayed to the other side of the tank, Spray went to her. Then Spray turned on her back, positioned the baby on her chest between her flippers, and rose to the surface, pushing the young one out of water. Other dolphin mothers have been seen to do this when their young infants swim evasively away. The effect is to temporarily immobilize the young one.

On March 16, Spray left the baby entirely alone during the feeding. On this date, the infant nuzzled its mother's side immediately after the feeding, but several minutes elapsed before Spray slowed down to allow her to suckle. On March 17, Spray allowed the infant to swim around alone for several ten-minute periods. On that day, the baby appeared to be nursing almost continuously, only very short intervals elapsing between periods of suckling.

On March 18, the baby left Spray several times, and sometimes entered another group of dolphins. Spray did not follow her, but allowed her to work her way out of the group alone.

During the morning of March 19, the infant alternately remained close to Spray and persistently suckled, or wandered far away from her, while Spray was occupied with other animals. At these times, Spray did not bring her back or swim after her. The baby was seen to suckle several times at 9:30 a.m.

At 12:15 p.m. it was reported to the observers that the infant was in distress, and both hastened to the tank. Unfortunately, by the time they arrived, a minute or two later, the infant was dead, and it was necessary to gather reports from eyewitnesses, and to attempt to fit together whatever facts could be supplied by them into a coherent account.

Early on the morning of the 19th, it was reported by an employee of Marine Studios that Spray and another unidentified dolphin, probably Mona, pushed the baby down to the floor of the tank. By moving their bodies over her, they temporarily prevented her from rising to the surface. There was no apparent reason for this action, and its significance is not clear. This report was substantiated by two other employees who happened to be looking into the tank at the time. Since both observers had seen the infant following this incident, and she appeared to be in good condition, no particular importance was attached to it at the time.

At about 12:06 p.m., the infant swam to the surface to breathe, apparently under her own power. Spray met her as she came down, and the two rose to the surface again, Spray pushing the young one up ahead of herself. As the baby sank, the second time bubbles of air streamed from her blowhole, and she did not swim again. Spray pushed her about the tank, nudging her up toward the surface every minute or so, but the infant did not breathe again. The baby's mouth opened and her tongue hung out to the side. The above account came from another employee who was watching through the porthole at the time, and it was at this moment that the authors arrived on the scene and it was observed that the baby was dead. A diver entered the tank immediately to bring her out. Spray actively avoided the diver and pushed the dead calf ahead of her, but the body was finally taken from her and removed from the tank. From the time the infant was first seen to be in distress to the time when she was removed from the tank, only 12 minues had elapsed. The body was taken to the laboratory and an autopsy was performed. This revealed that the calf was extremely thin, her stomach was completely empty, and she had suffered a fractured left mandible. Her lungs contained water, and it was therefore assumed that the immediate cause of death was drowning. Judging from the extremely fresh condition of the fracture, it is believed that the accident that caused it must have taken place within 24 hours of her death. At the time of her death at the age of 15 days, the infant measured 42.5 inches in total length, and weighed 30 pounds. Her weight may have been slightly less than normal for her age, since she was very thin. She possessed eight hair follicles on the left side of her snout, and six on the right side, but only one vibrissa was visible, in the last hair follicle on the right side. No structural abnormalities were found at the autopsy.

Whatever the reason may have been, Spray's infant was not receiving the usual amount of care that is given to newborn dolphins. Her mother left her for unusually long periods of time, and failed to remove her from situations in which she might have been injured inadvert-

ently by the other animals. On March 13, the baby swam directly under the platform while the other animals were feeding, and was struck by at least one dolphin falling back into the water. On March 18, while Pudgy and the bull were engaged in some of the more vigorous courtship activities, the baby swam between them, and may have been lashed by a tail before she found her way out. In neither of these instances did Spray make any attempt to rescue her young one, and it is possible that the latter incident was the cause of the infant's fractured mandible.

Two of the 1953 infants died before the end of their first year, one by accidental drowning, and the second because of an unknown infection, on which an investigation is being carried out at the present time. The remaining two young dolphins born in February, 1953, were weighed and measured in September of that year, and their lengths at that time were 68 and 69 inches, their weights 146 and 141 pounds. At the present writing they are 16 months old. They still nurse regularly, usually after feeding time, although it is thought that they are about to end the nursing period, since they occasionally skip a nursing. They began to take small pieces of squid in August, 1953, and early in December they were observed to swallow fish for the first time. Since then both young dolphins have developed excellent appetites for fish and eat them regularly at feeding times. The nursing period usually ends gradually over a period of months as the young animals show an increasing preference for fish. They race the adults for the fish even after their appetites have been satisfied. They have often been seen to rush for a fish thrown to them, then drop it to race after another on the other side of the tank. They seem to make a special effort to take fish from just in front of another animal, and often do so. They may play with the fish so taken in a number of ways. They will drop a dead fish in front of the rocks where the small tank inhabitants hide, and just as they come out to eat, the young dolphin will snatch the fish away again, only to repeat the performance a minute later. The young animals indulge in this type of sport only after they have eaten and are satisfied, but often the fish are caught by a still hungry adult and the youngsters are deprived of their plaything. Every activity of the young animals now in the tank shows them to be normal healthy dolphins.

Discussion

The dolphins are a specialized group of mammals adapted in both structure and function to a life lived completely in the water. Superficially, they resemble fish. Their forelimbs are flippers, without use as grasping organs, and probably serve mostly as balancers, or in steering. They possess no hind limbs. Their tails, furnished with broad horizontal flukes, are excellent propulsive organs. Their streamlined form enables them to move gracefully and rapidly through the water.

Since they were derived from land mammals, they bear their young alive in typical mammalian fashion, and suckle them for an extended period of time. They also display mammalian care for the young. Since they possess no limbs which can be used as manipulative organs, their mouths, which are provided with a set of efficient teeth for holding their prey, serve also to grasp objects and to inflict wounds in their own defense. The powerful muscles of the tail also aid in defense.

Together with these features, the dolphin possesses a highly developed and exceptionally large brain, of which the largest part is cerebrum. The brain of one nine-months-old *Tursiops* weighed 1230.4 grams, and its volume was 1225 cc. The length of this male specimen at the time of its death was 64 inches, and its weight was 137 pounds.

The large brain and the probable resulting high level of adaptiveness might be expected to lead, in animals with manipulative limbs, to complex varieties of behavior. The lack of these limbs results in the ingenious use of flukes and flippers. These can be delicately adjusted to produce minute changes in movement and position. Such changes enable the animal to make the best possible use of the only grasping organ it possesses, the mouth. The remarkable use of these organs under the control of a well-developed central nervous system leads to behavior patterns which are peculiar to these animals and their close relatives.

No accurate observations on the precopulatory and copulatory behavior of dolphins were possible before the tanks at Marine Studios were established, and therefore such observations as were available were recorded by whalers and transmitted to interested scientists, or such scientists reported their own observations from the decks of ships. Lillie (1910) reported that whalers saw two adult sperm whales (*Physeter*) rush together near the surface, then turn up vertically at the end of the rush. They believed that they had seen copulation, and said that the males were exhausted and easy to capture after these activities. Morch (1911) observed coition in blue whales during the summer, but gave no details of their behavior. Tomilin (1935) noted what he considered to be sexual attachment in various species, and differences between the species and

between individuals in the same species. He stated that this attachment sometimes reached great intensity and was strongly shown especially if one of a pair was wounded. He gave no details of copulation. Hamilton (1945) reported that while sailing off the coast of Brazil, he saw two *Steno* swimming on their sides with their genital areas pressed together. They were slightly separated anteriorly, and one's mouth was slightly open. This posture was maintained while they remained in sight, which, according to the author, was "not for very long." The ship was moving at 10 knots, and the animals maintained the speed of the ship while in the above position.

Such fragmentary observations do not give any indication of the complex pattern of precopulatory and copulatory behavior in this group of animals and it was not until they could be observed under water for extended periods of time that details could be reported. Although many of the events leading to copulation are reported here, the sequence is variable, and it is by no means certain that copulation can be predicted following any particular stage. The observers have seen much copulatory behavior, some of it at least partially successful. In at least one instance an ejaculation of semen has been seen after withdrawal of the penis from the vagina of the female. Sudden erection and retraction of the penis occur most often during the spring months both with and without true copulatory activity, so that retraction is no indication that ejaculation has taken place during a partial intromission. The one instance in which full penetration took place occurred before seven in the morning and was not seen by the authors. The employee who witnessed it is a reliable observer who has made a hobby of watching the animals over a long period of time. It is not known whether the copulations involving partial penetration over a short time are as effective as those with full penetration extending over 30 seconds. Although the authors have spent a number of hours watching during the evening hours and also in the early morning, they have not seen the longer copulations. Since there is no provision for adequate lighting at night, observations during this time are impossible. Perhaps long-continued early morning observations over a long period of time will provide more data.

Although McBride, in 1940, recognized the jaw clapping of the bull as "the principal form of intimidation," the entire use of this sound was not recognized until much later. As late as 1948, McBride & Hebb again stated that this sound was used by a dominant animal toward subordinates. The observations of the present authors indicate that this is not always the case, and the jaw clap has, under direct observation, been made or attempted by almost every animal in the tank. It has occurred under a number of circumstances but these were always such that the jaw clapping animal appeared to be displeased, dissatisfied or annoyed. Pudgy clapped her jaws when the bull, who is dominant to her, made sexual advances to her and she was not responsive. All the mothers clapped their jaws when another animal interfered with or approached their young. Spray has been seen to clap her jaws when the young male swam between her and the infants in her company. The younger animals, such as Spray and the young male, produce a much less resounding clap than Pudgy and the bull, but their efforts were unmistakeable, and as they gained more experience and practice, the sound produced became louder. Apparently this evidence of displeasure is limited to the adults, since the 1953 youngsters have not as yet attempted it.

Townsend (1914) gives some evidence to show that *Tursiops* breeds yearly in the wild. Of 51 specimens taken in November, 34 were females. All the females taken were in milk at that time. Although he does not state how many of the females were killed, all those that were killed were not only in milk but contained young. Unfortunately, the age of the suckling infants could not be determined. Therefore, it is not known whether all infants in the wild suckle for 18 to 21 months or more, or whether there is a yearly reproductive cycle. Since young dolphins at Marineland have been known to suckle for periods up to 20 months, it is possible that Townsend's data would support the idea of a two-year cycle in the wild.

At Marine Studios, no female has as yet produced young two years in succession. Several animals have produced young at two-year intervals. There is in the tank only one fully adult male, and therefore no significant competition for females. There is the possibility that females unaccompanied by newborn young are preferred partners. It is to be hoped that some future study may show whether the two-year cycle seen at Marine Studios is unchanged from the wild condition.

McBride & Kritzler (1951) believed that the female Bottle-nosed Dolphin becomes sexually mature at four years of age and may bear her first infant in the spring of her fifth year. Although this may be theoretically true, the only evidence now at hand indicates that the first infant may not be conceived until several years later. Spray, the only animal that was born and reached sexual maturity in captivity, did not conceive until she was six years of age, and

delivered her first infant just after her seventh birthday, although she was known to be in excellent condition throughout her life. It is, of course, not known whether she would have conceived earlier in the wild, and further evidence on the age at which sexual maturity is reached will depend on the time at which the young females now in the tanks first conceive.

There has been much speculation on the length of the gestation period in these animals, and estimates which have run from 10 to 14 months have in the last few years narrowed to 11 to 13 months. It is now possible to state with a reasonable degree of accuracy that the gestation period is very close to 12 months. Spray's association with the bull lasted for a period of two weeks, from February 23 to March 9, 1953, and her infant was born on March 4, 1954. Similarly, the associations of Mona and Susie with the bull were almost exactly a year before the birth of their young ones. Although Pudgy was observed to be in the company of the bull in late April, 1952, and her infant was born in early May of the following year, the authors believe that this discrepancy comes within the limit of error, and that the twelve-month period is the most valid one.

McBride & Kritzler (1951) noted the withdrawal from association with other animals shown by pregnant females, especially during the latter part of pregnancy. They also mentioned the tendency of two pregnant females to associate with each other. These tendencies have been confirmed in the present paper. In 1952, Pudgy and Mrs. Jones, although they conceived several months apart, spent most of their time together during their pregnancies, though they had not been close companions before this time. When Pudgy's infant was born, Mrs. Jones was the animal which escorted the infant during the first few minutes of its life, and she and Spray kept the infant out of the way of other excited animals, and accompanied Pudgy and the new baby for the first few weeks. When Spray's infant was born it was Mona, her mother, and Pudgy who performed these functions alternately, so that there was almost always another mature female swimming beside the baby. Such protection proved to be important, since the records show that the birth of a young one seems to stimulate the adult male to begin or renew his courting activities. Often these are directed toward the new mother, whose evasive movements become frantic in her efforts to protect her newborn infant. In 1947, when Spray was born, there were several adult males in the tank, and in their attacks on the new mother and other females and each other, Spray's skin was badly lacerated by their teeth. Since then, these competing animals have been removed, but the danger to the new infants still exists, though to a lesser degree.

In one case, however, the new mother was not accompanied by another female. Susie is an extremely retiring animal, and remained alone from the time she was first captured and placed in the tank. She conceived in February, 1952, and remained alone throughout her pregnancy, a situation which was unusual enough to warrant the attention of the observers. When her infant was born in February, 1953, she was not accompanied by any other animal. Immediately after the birth Pudgy made persistent efforts to swim with her and remain near her, but Susie avoided Pudgy as diligently as she did all the other animals. Her behavior, though unusual, was consistent, since both before and after her pregnancy she showed no inclination to associate with any other dolphin. She was captured in 1949 and gave birth three days later to a male infant, an event which took place in the receiving tank. This tank contains very shallow water, and the environment was quite unnatural to her. Her timidity may have stemmed from that time. The young male has now almost reached maturity, and the two ceased their association prior to the arrival of the new infant. It took more than a year of training before Susie took her food at the feeding platform. Either her inherent timidity or the shock of her arrival and the subsequent birth may account for her unusual conduct.

The young of members of the Delphinidae are usually born tail first. In every birth at Marine Studios except one (Spring, 1955) the infant emerged in this manner.

In the earliest papers describing the birth of small cetaceans, (James, 1914), the author assumed that the normal presentation was head first, and that it was mishandling or other improper treatment which caused the tail presentation. The birth described by James took place in *Phocaena phocaena* and was a stillbirth. James mentioned mishandling as the reason for the tail presentation, and the tail presentation as the reason for the stillbirth. It is now known that although mishandling my lead to stillbirth, the reasons are other than those described above.

Caudal presentation has been described in detail by a number of authors (Wislocki & Enders, 1941; Slijper, 1949). McBride & Kritzler (1951) discussed it in connection with data available to them from Marine Studios, and all agree that the foetus is, or becomes, oriented in such a way that the head is pointed toward the tubal end of the uterine cornu, while the tail extends toward

the vaginal opening. Sleptzov (1940) observed 635 embryos of *Delphinus delphis* in situ during various stages of development, and came to the conclusion that during early embryology the foetus may lie in either direction. Later the head tends to become oriented toward the tubal end of the cornu, and by the time reversal is no longer possible, because of size, the vast majority of embryos are situated in this way, so that tail presentation is inevitable.

The problem remains, however as to why the orientation takes place in this manner. Slijper (1949), citing Williams & DeSnoo, discusses the dangers attendant upon breech presentation in mammals which produce foetuses with comparatively large heads, and believes that the compression of the umbilical cord between the pelvis of the mother and the head of the infant which occurs in breech presentation may cause asphyxia if the infant is not quickly extracted. Although Odontocetes possess no pelvic girdle other than two small pelvic bones, the pelvic region contains large masses of tough fibrous connective tissue which could exert considerable pressure, and it is possible that such compression may be exerted in the case of these animals. Whether or not this is true, it does not explain the orientation of the foetus in the uterus, but only illustrates an effect of such orientation.

Slijper's discussion of the role of uterine contractions in the orientation of the foetus is more pertinent to the question. Mammals other than primates show, during pregnancy, uterine contractions of a peristaltic nature which begin at the tubal end of the uterus, and Slijper believes that the head should be impelled in the direction of the cervix under the influence of these contractions, in mammals with a small head and long neck. Since this formation does not apply to cetaceans, he considers that the body form of the foetal cetacean might favor caudal presentation.

Schumann (1914) discusses the possible causes of almost universal cephalic presentation. He states that in multiparous animals the foetuses lie indifferently, in either breech or cephalic presentation, whereas in unipara, the head presents in 90 to 98 percent of the cases. In man the foetal head is heaviest and gravitates to the most dependent position, nearest the cervix. In uniparous quadrupeds, however, the hindquarters and trunk of the foetus are its heaviest parts, and consequently sink to the lowest portion of the uterus, which with its cornua lies low in the abdominal cavity. The cervix rises to meet the vagina.

In dolphins, which are uniparous, the uterus lies in a situation similar to that seen in the quadrupeds, so that the heaviest portion of the foetus would tend to gravitate to the lowest portion, the tubal end of the cornu. These animals, however, possess no hind limbs, only remnants of the pelvic girdle, and the tail is long and slender. The head, which is relatively very large, and the pectoral region are heavier than the hindquarters. Under these circumstances, the gravitation of the heaviest portion toward the tubal end of the uterus would result in tail presentation. The present authors believe that this situation may be of considerable influence in the determination of tail presentation in the dolphins.[4]

It is necessary, however, to consider the folding of the uterine cornu in evaluating this explanation. The non-pregnant dolphin uterus is not folded. Presumably the fold occurs when the foetus is too long to extend to its full length in the abdomen of the mother. At this time it would also be too large to turn easily on its own axis. Examination of the pregnant uterus of many delphinids has shown that the foetus appears, at first glance, to have its head oriented toward the vaginal end of the uterus. Closer observation, however, has usually shown that the head is enclosed in a fold, which is oriented toward the caudal end of the mother, but that on following this fold in the direction in which the head is pointing, it is found that the uterus continues from this point toward the Fallopian tubes. Following the body of the foetus in the opposite direction reveals that it folds close to the origin of the tail, and the tail occupies the lower end of the uterus, and extends toward the vaginal opening.

These facts may seem to contradict the weight theory outlined above, but if we consider that the head of the foetus, as in most mammals, develops more rapidly than the other parts, and becomes the heaviest part of the foetus in an early stage of development, before the fold occurs, it seems possible that both events might occur in sequence, with the usual observed result of tail presentation. It is unfortunate that Sleptzov (1940), who had at his disposal more than six hundred foetuses in all stages of development, did not record more fully the sizes, weights and developmental characteristics of these animals, together with the condition and configuration of the uteri in which they were found.

Although McBride & Kritzler (1951) stated that in all cases observed by them the dorsal fin of the newborn dolphin was folded to the right,

[4]Recently E. J. Slijper (1956. Some remarks on gestation and birth in cetacea and other aquatic mammals. Hvalrädets Skrifter. Scientific Results of Marine Biological Research, No. 41, pp. 1-62) reported additional data and conclusions concerning tail presentation in cetacea which confirm those given above.

at least two cases were seen by the present observers in which the dorsal was folded to the left. In one of these cases the infant was seen to be lying on its left side when only partly extruded from the mother's body. We do not know whether this correlation holds true in all cases.

The symmetrically placed vertical creases on each side of the trunk at birth are not necessarily six in number, as stated by McBride & Kritzler. In the group of births recorded here, the creases have numbered five, six or seven, and there were sometimes more on one side than on the other. Also, one or more may be continuous over the dorsal part of the animal. They lacked pigment and were easily visible for several weeks after birth, when they gradually acquired pigment and disappeared. The young dolphin to which Spray gave birth, and which died at 15 days of age, showed two creases which were not continuous over the dorsal side but which appeared on both sides, three which were continuous over the dorsal, and two ventral creases, which were not seen previous to her death because of the lack of pigment on the ventral side of the body.

It may be significant to note that the dorsal fin of the infant which died at 15 days was slightly inclined to the right when the body was removed from the tank. At birth it was distinctly folded to the left. It has been noted by many observers that the dorsal fins of all the adults incline to the right, and it is thought that the swimming tendencies of the animals may be the cause of this phenomenon. Since the animals in the tank usually swim in a clockwise direction through a counterclockwise current, the force of the water against their dorsal fins may be the cause. It should be noted, however, that this inclination in no way hampers their swimming in any other direction. It seems significant that the tilt to the right should have taken place so quickly in an infant whose dorsal was inclined sharply in the opposite direction only 15 days before.

The mother of a newborn dolphin has never been seen to eat the placenta, which is expelled several hours after birth. Since eating this organ appears to play a significant role in the behavior of so many other mammals, this point seemed to be of particular interest. In all the cases on record at Marine Studios no mother dolphin has even approached the placenta after expelling it, and unless removed by divers and preserved, the organ is torn to shreds by the turtles and fish in the tank.

Although McBride & Kritzler (1951) reported that a mother dolphin, immediately after the infant's body falls free, will whirl about and thus snap the umbilical cord, this does not appear to be necessary in every case. At least one female in the present group spurted forward in a straight fast swim as the baby was released and the cord snapped quickly as it pulled taut. The survival value of the whirl, in case the infant fails to reach the surface, is obvious, but the pattern does not seem to be an invariable one.

The problem of suckling in the dolphin has long been of interest to observers, and the mechanism has been fairly well worked out. Milk is poured from the mammary glands into large sinusoids, which in turn open to the nipples, situated on each side of the genital slit. When the infant grasps the nipple, abdominal contractions of the mother pour the secretions into the baby's mouth. The question remained as to whether the stimulation of the nipple by the infant was necessary in order to produce a flow of milk, or whether the contraction of the abdominal muscles was under the voluntary control of the mother. An instance that took place in the spring of 1954 shows that, at least in extraordinary circumstances, the flow of milk is entirely under the mother's control. On February 22, 1954, a nine-months-old young dolphin, born the previous May, died at Marine Studios of an unknown skin infection. At the time of his death, he was still getting the main part of his food from his mother, and was only beginning to show an interest in other food. On the day before his death, he suckled very few times, and his mother's nipples protruded from their slits, apparently pushed outward by the engorged sinusoids. On the day of his death and for several days afterwards this condition continued. Twice in the first several days after the young one's death, the mother was seen to turn on her side in the water and visibly contract her abdominal muscles, raising her tail as she did so. As she did this, a stream of milk spurted from her nipples. This stream was ejected with a force strong enough to send it a distance of more than two feet before it dissipated into the water. It is not known whether such a feat can be accomplished in circumstances where the sinusoids are not filled to excess, but it shows that a female dolphin can eject milk without stimulation of the nipple under certain conditions.

Several Russian authors, particularly Khvatov (1938) and Sleptzov (1940) have reported on births of Delphinidae (mainly *Delphinus delphis*) which they observed in the Black Sea. In most of these births, the animals concerned were captured dolphins, and were seen while in seines being drawn toward shore. The rest were in shallow areas near shore. It is possible

that the births may have been abnormal in some cases, particularly in the case of the captured animals, which could have been shocked and frightened by the procedure of capture. Also the conditions for observing the births were unfavorable, since many animals were milling about in the seine, and in all cases the births were observed from above the surface of the water. In spite of these difficulties, there are descriptions of reverse flexions, leaps, dives, and in some instances, the moment of birth when the infant fell free. In all cases the infant was born tail first, but no description of the moments immediately following birth is recorded. In the most complete description, the birth took one hour and fifteen minutes from the time the author (Sleptzov, 1940) first saw the tail of the infant protruding from the mother, and the infant's dorsal fin was folded to the right. The general description of the birth is similar to those seen at Marine Studios. Khvatov, after seeing an apparently abnormal birth, observed an infant attached to its mother by the umbilical cord, and postulated that this was a normal condition. He thought that the infant suckled while still attached to the mother. In the speeimens examined at Marine Studios, no umbilical cord was found to be long enough to permit such a procedure. Whether the umbilical cord of the species he studied was sufficient in length is not known, but Sleptzov, after seeing what he believed to be the same species, thought Khvatov's theory erroneous. He observed a larger number of births than did Khvatov, and in each instance the infant separated from the mother promptly with no apparent ill effects to either. All evidence from births in the wild indicates that they parallel closely those seen at Marine Studios.

The reaction of Spray toward her first infant presents an interesting problem. She was seven years of age when she gave birth to this calf. It has been thought that dolphins mature sexually at an earlier age, and therefore it is doubtful that she was too young to care for it. She had been active for several years in escorting and protecting other young dolphins in the tank and it seems reasonable to assume that therefore she had sufficient general background experience. However, never before had she had the constant care of an infant, and she had not suckled an infant before. Although the immediate cause of the infant's death was drowning, it is not certain whether the baby drowned because of a shock reaction to the fractured mandible, whether it starved until it was too weak to swim, or whether there was another reason, undiscernible to the investigators. The observers could find no abnormalities in the digestive tract to account for its thinness or its inability to suckle. Young dolphins use their tongues, rather than their lower jaws, in suckling. The youngster was quite obviously hungry, judging from the number of times it approached its mother's mammaries, and its persistent nuzzling there. It was impossible to determine whether Spray produced sufficient milk as she could not be removed from the tank for examination. Her mammary glands remained distended for several days and gradually receded over a period of several weeks. It is possible that more evidence may be found when Spray gives birth to a second infant and her reactions to it can be observed.

Although this report contains many data that have not been previously presented, it is extremely difficult to quantify, since records of the earlier births, both by McBride and his coworkers and by the present investigators, did not contain all the details which are now considered essential to an analysis of the behavior of these animals. In addition it is probable that further details, up to now unrecorded, will later present themselves. Further observation by experienced investigators and the recording of seemingly non-essential details will produce a more complete picture, and one that will allow a more accurate comparison with other mammals.

Summary

The group of captive Bottle-nosed Dolphins (*Tursiops truncatus*) at Marine Studios is an actively reproducing colony. Mating and parturition take place from February to May, usually in a two-year cycle. The report comprises the data on five pregnancies and births, one of which was observed from conception.

Precopulatory behavior consisted of a prolonged companionship between a male and female. There followed such activities as posturing, stroking, rubbing, nuzzling, mouthing, jaw clapping and yelping on the part of the male. These occurred in any sequence and if the female responded, copulatory behavior followed. This included erection, approach, intromission, ejaculation and withdrawal. Most of the copulatory activity took place at night or in the early morning, although some of the activities were seen at all hours during the day.

The gestation period was about twelve months. After about four or five months, the pregnant female tended to withdraw from the society of other dolphins, and usually established at this time the one or two associations which she maintained throughout the remainder of her pregnancy. The rest of her time was spent alone. Her activities gradually diminished in vigor, and as term approached she became slow and sometimes clumsy. Toward the end of preg-

nancy a labored respiratory pattern was seen, yawning and body flexion appeared, and defecation increased in frequency.

The infants were born tail first. The mother either whirled or swam rapidly ahead, and the umbilical cord broke as it pulled taut. The unpigmented creases on each side of the body of the infant were not symmetrical in every case, and sometimes there were more on one side than on the other. The infants swam from birth. The dorsal fin was folded sharply either to the right or left, but stiffened in an upright position within a few hours. The placenta was expelled several hours after birth. The mother did not eat it, nor did she approach it again.

Dolphin mothers kept close to their infants at all times for the first months, and removed them promptly from dangerous situations. During the first weeks, the infants were not allowed to stray more than ten feet from the mother. Nursing was established during the first 24 hours. The infants were weaned at approximately 18 months.

One female dolphin, born and raised at Marine Studios, did not care for her infant as carefully as the other mothers. She left the baby alone at feeding time and for other short periods. She did not remove it from contact with other animals or from dangerous situations. The infant died at 15 days of age.

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EXPLANATION OF THE PLATES*

Plate I

Fig. 1. Young male dolphin (Algie) above, and adult female (Mona) below. The male strokes the back of the female with his flippers.

Fig. 2. Young male and female during rubbing activity. The two have approached each other head-on and their bodies will rub together (Algie and Spray).

Fig. 3. Young male and female during rubbing activity (Algie and Spray).

Fig. 4. Male and female during mouthing.

Fig. 5. Adult male (Happy) and young female (Spray) in copulation. Note partial insertion of penis into vaginal opening.

Plate II

Fig. 6. Adult female (Susie) in non-pregnant state.

Fig. 7. Adult female (Susie) in late pregnancy.

Fig. 8. Adult female (Mrs. Jones) in late pregnancy, in body flexion.

Fig. 9. Adult female (Mona) in late pregnancy. Recurve of body flexion.

Fig. 10. Female in late pregnancy. Recurve of body flexion while rubbing over rocks. Note vaginal distension and protruding nipples.

Fig. 11. Birth in progress. Flukes and part of caudal peduncle are seen projecting from vagina of mother.

Fig. 12. Birth in progress. Taken just before complete emergence. Note umbilical cord, also presence of companion female on the left.

Plate III

Fig. 13. Suckling. Young female (Spray) and infant (Peggy) a few days after birth.

Fig. 14. A new mother (Pudgy) escorts her own infant and two others during feeding period while mothers of the other two feed.

*Photographs by F. S. Essapian.